Experimental Studies on Heredity in Rabbits. (Assisted by the Elizabeth Thompson Science Fund.) By C. C. Hurst, F.L.S.

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The following experiments were designed in 1902 with the object of determining whether the Mendelian principles of heredity were applicable to animals as well as plants. For that purpose the domestic Rabbit seemed to be a likely subject, as many of the fancy races were well known to possess distinct structural and colour characters which constantly bred true.

At first, in order to make the experiments as simple as possible, two races only were selected for crossing, White Angora and Belgian Hare. The former is an albino race with pink eyes, swaying habit, and a long Angora coat of fine texture; while the latter is a normal race with pigmented skin, dark eyes, and short yellow-grey fur of coarser texture. An inbred pair of each race was crossed reciprocally, and the hybrids of the first generation were all normal individuals with pigmented skin, dark eyes, short fur, and grey coat like that of the common wild rabbit. Those by the albino buck were all self-coloured, while those from the albino doe were, with one exception, more or less marked with white on the fore extremities. These grey hybrids bred together produced 14 distinct types in the second generation, viz.:—

Short, normal *, grey, self-coloured.
Short, normal, grey, marked.
Short, normal, grey, Dutch-marked.
Short, normal, black, self-coloured.
Short, normal, black, marked.
Short, normal, black, Dutch-marked.
Short, albino †, white.
Angora, normal, grey, self-coloured.
Angora, normal, grey, marked.
Angora, normal, grey, Dutch-marked.
Angora, normal, black, self-coloured.
Angora, normal, black, marked.
Angora, normal, black, Dutch-marked.
Angora, albino, white.

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* Pigmented, with normal demeanour (see p. 292).

† Unpigmented, with swaying habit (see p. 292).

All the normals had dark eyes and the albinos pink eyes. Several types appeared in the same litter, and each individual hybrid produced all the types.

This epidemic of variation in the second generation of hybrids has been the common experience of experimenters both in animals and plants, and before the Mendelian principles became known remained practically unexplained. By the aid of the Mendelian principles we are able to see at once that there are at least 4 pairs of distinct characters concerned in the offspring of the second generation, each pair being inherited independently of the others, viz.:—Short and Angora coat, normality and albinism, grey and black coat, self-coloured and marked coat.

In order to simplify such a complicated problem, each of these 4 pairs of characters will be dealt with singly, and the offspring of each individual detailed separately. To facilitate this, each individual was numbered as soon as it was used at the stud, which number is reserved solely for that individual throughout its life.

The 4 individuals used at the outset were as follows:—No. 1 doe and No. 4 buck were pure bred Belgian Hares raised out of the same litter. No. 2 buck and No. 3 doe were pure-bred White Angoras, both by the same buck but out of different does.

These 4 individuals were obtained from local fanciers, whose pure and constant strains had been under observation for several years, so that no extensive tests of their purity and constancy were deemed necessary. For the purpose, however, of securing young stock for further experiments, 4 litters, containing 28 individuals, were raised from the pair of Belgians and the pair of Angoras; all of these bred true to their parents in all the characters with which we are concerned.

(1) SHORT AND ANGORA COAT.

The coat of the "Belgian Hare" rabbit, in common with that of the wild rabbit and most of the domesticated races, is made up of short coarse fur, the longest hairs of which seldom exceed one inch.

The coat of the Angora race consists of long, fine wool, the longest hairs of which often exceed six inches.

The two kinds of coat are unmistakable, not only in the extreme difference in their length, but also in their texture. The Angora coat is finer and softer in texture than the short coat, and, unless constantly combed out, quickly becomes matted and woolly, unlike the short fur, which lies back quite flat.

As already noted, both kinds of coat breed true when mated with their own kind.

(a) *First Generation* (F_1).

No. 1 doe with short coat mated with No. 2 buck with Angora coat produced 26 hybrids with short coats.

The reverse cross, No. 3 doe with Angora coat mated with No. 4 buck with short coat, produced 16 hybrids with short coats. In general appearance the hybrid short coats were indistinguishable from the pure short coat, the influence of the Angora character not being apparent. A careful examination, however, revealed what appeared to be faint traces of the Angora influence in both length and texture. The hairs of the hybrid coat were slightly longer, seemed softer to the touch, and were apparently more densely distributed than in the pure short coat. At the same time it must be admitted that these apparent traces of the Angora influence were so small, that had one not known the Angora parentage it would never have been suspected. In Mendelian terms, therefore, short coat may be said to be dominant over Angora coat, which is recessive.

Further experiments recently carried out show that the short coat of other races, as well as the Belgian Hare, is similarly dominant over the Angora coat. Altogether, 87 hybrids have been raised by crossing shorts with Angoras, and all have short coats, no matter whether the Angora was used as the male or female parent. It appears, therefore, that in these cases the phenomenon of dominance is peculiar to the character itself, and is not in any way influenced by change of sex, change of individual, or change of race.

The following table gives the results of the individual matings. S = pure short coat, A = pure Angora coat, and the numbers attached to these letters refer to the individual animals used. To save repetition, it may be noted that the doe is placed first throughout the matings; *e. g.*, S 1 × A 2 is No. 1 doe with short coat mated with No. 2 buck with Angora coat; Nos. 1, 4, 13, and

25 are Belgian Hares, No. 47 is a Silver Fawn, Nos. 51 and 52 are Dutch, No. 61 is a Himalayan, and Nos. 2, 3, 23, and 50 are Angoras.

Table 1.

Shorts × Angoras (F_1).

Matings.	*Short.*	*Angora.*
S 1 × A 2	26	0
A 3 × S 4	16	0
A 3 × S 51	8	0
S 13 × A 2	4	0
A 23 × S 25	13	0
A 23 × S 61	7	0
A 50 × S 47	8	0
S 52 × A 2	5	0
Total	87	0

(b) *Second Generation* (F_2).

The short-coated hybrids of the first generation bred together produced a mixture of shorts and Angoras in Mendelian proportions. 7 short-coated hybrids bred together produced 171 young, of which 70 were reared to the age of two months or more, when the nature of the coat became evident; of these, 53 had short coats and 17 were Angoras.

The Mendelian expectation for 68 young is 51 shorts and 17 Angoras.

The Angora coats of the second generation were indistinguishable from those of pure-bred Angoras of the same age.

The short coats of the second generation were similar in appearance to those of the pure and hybrid shorts.

Each individual hybrid of the first generation that was tested produced both kinds of coat, usually in the same litter.

The individual results were as follows :—No. 5 gave 6 shorts and 3 Angoras ; No. 7, 8 S and 3 A ; No. 8, 2 S and 2 A ; No. 9, 24 S and 5 A ; No. 10, 37 S and 11 A ; No. 11, 13 S and 4 A ; No. 12, 16 S and 6 A.

The following table gives the individual matings with the details of each litter. H = hybrid of the first generation bred from S × A.

TABLE 2.

Hybrid Shorts bred together (F_2).

Matings.	*Short.*	*Angora.*
H 5 × H 12	5	2
H 5 × H 10	1	1
H 7 × H 10	2	1
H 7 × H 10	2	1
H 7 × H 10	4	1
H 8 × H 10	1	1
H 8 × H 10	1	1
H 9 × H 10	7	1
H 9 × H 10	5	2
H 9 × H 10	2	1
H 9 × H 10	4	0
H 9 × H 10	6	1
H 11 × H 12	5	2
H 11 × H 12	6	2
H 12 × H 10	2	0
Total	53	17

The short-coated hybrids of the first generation mated back with the original Angoras produced a mixture of shorts and Angoras in Mendelian proportions. 5 short-coated hybrids mated with Angoras produced 54 young, of which 38 were reared; of these, 20 had short coats similar in appearance to those of the pure and hybrid shorts, while 18 were Angoras indistinguishable from the pure Angoras. The Mendelian expectation for this mating is 19 shorts and 19 Angoras.

Curiously enough, in the first litter H 8 × A 2 produced 5 young, *all Angoras*, while in the second litter there were 3 shorts and 3 Angoras, as expected. The following table gives the numbers obtained in each litter from the individual matings :—

TABLE 3.

Hybrid Shorts × Angoras (F).

Matings.	*Short.*	*Angora.*
H 5 × A 2	3	2
H 5 × A 2	5	2
H 7 × A 2	4	3
H 8 × A 2	0	5
H 8 × A 2	3	3
A 3 × H 10	3	3
A 3 × H 12	2	0
Total	20	18

2 short-coated hybrids of the first generation mated back with the original short produced 20 young, of which 17 were reared. All had short coats similar in appearance to the pure and hybrid shorts, in accordance with the Mendelian expectation.

The matings were as follows :—S 1 × H 12 gave 11 shorts in two litters, and S 1 × H 10 gave 6 shorts in one litter.

(c) *Third Generation* (F_3).

The Angoras of the second generation extracted from the hybrid shorts of the first generation bred quite true when mated together and with pure-bred Angoras.

9 extracted Angoras mated together and with Angoras produced 41 Angora young, all indistinguishable from pure-bred Angoras, in accordance with the Mendelian expectation. 26 of these were raised from the extracted Angoras bred together.

The individual matings were as follows. E A = Extracted Angora. Nos. 26, 33, 37, 53, and 54 were extracted from H × H, while Nos. 16, 20, 41, and 42 were extracted from H × A.

TABLE 4.

Extracted Angoras × Angoras (F_3).

Matings.	*Short.*	*Angora.*
E A 16 × A 2	0	5
E A 20 × A 2	0	4
E A 33 × A 24	0	6
E A 33 × E A 37	0	7
E A 42 × E A 26	0	6
E A 53 × E A 37	0	7
E A 54 × E A 41	0	6
Total	0	41

The extracted Angoras, like the pure-bred Angoras, proved to be recessive to pure shorts. 4 extracted Angoras mated with 3 pure and 1 extracted short produced 27 short-coated young, similar in appearance to the pure and hybrid shorts.

The matings were as follows (E S = Extracted pure Short):—

TABLE 5.

Extracted Angoras × Pure Shorts (F_3).

Matings.	*Short.*	*Angora.*
E A 15 × S 25	6	0
E A 15 × S 51	8	0
E A 16 × S 61	7	0
E S 34 × E A 37	6	0
Total	27	0

The extracted Angoras, like the pure-bred Angoras, gave a mixture of shorts and Angoras when mated with hybrid shorts. 5 extracted Angoras mated with 3 hybrid shorts produced 28 young, of which 17 had short coats and 11 Angoras. The Mendelian expectation is 14 shorts and 14 Angoras.

It will be observed that there is here a slight excess of shorts, which appears to be due to E H 28 giving 12 shorts and 6 Angoras instead of the expected 9 of each. The matings were as follows:—

TABLE 6.

Extracted Angoras × Hybrid Shorts (F_3).

Matings.	*Short.*	*Angora.*
E A 15 × H 12	2	2
E A 15 × E H 28	3	1
E A 16 × E H 28	4	2
E A 16 × E H 28	1	0
E A 20 × E H 28	2	2
E A 33 × E H 28	2	1
E H 31 × E A 26	3	3
Total	17	11

From the above experiments with 10 Angoras extracted from hybrid shorts, it is clear that the extracted Angoras are not only indistinguishable in appearance from pure-bred Angoras, but in their breeding they behave exactly as do the pure-bred Angoras, viz.:—(1) They breed true with one another; (2) they are recessive to pure shorts; (3) they give mixed offspring when mated with hybrid shorts.

These facts are all in accordance with the Mendelian conception of gametic purity, and there seems to be no doubt that, notwithstanding their hybrid origin, these extracted Angoras are pure Angoras, giving off gametes carrying the Angora factor simply, with no trace of the short-coat factor carried (in the case of 5 of them) by both their parents and one-half of their ancestors for several generations and probably many more.

The short-coated individuals of the second generation tested with Angoras and hybrids proved to be of two kinds, pure shorts and hybrid shorts, the former producing all shorts and the latter a mixture of shorts and Angoras.

Out of 16 individuals tested, 5 were extracted from hybrids of the first generation mated back with the original Angoras (H × A), and these all proved to be hybrids in accordance with the Mendelian expectation.

One individual was extracted from a hybrid of the first generation mated back with one of the original shorts (H × S), and this proved to be a hybrid, the Mendelian expectation for 2 such individuals being 1 pure and 1 hybrid.

The remaining 10 individuals were extracted from hybrids of the first generation bred together (H × H), and of these 4 proved to be pure and 6 were hybrids; the Mendelian expectation for 12 such individuals being 4 pure and 8 hybrids.

The 4 pure extracted shorts mated with 3 Angoras and 4 hybrids produced 51 short-coated young, similar in appearance to the pure and hybrid shorts. The matings were as follows:—

TABLE 7.

Extracted Shorts × Angoras and Hybrids (F_3).

Matings.	*Short.*	*Angora.*
E S 30 × H 10	5	0
E S 30 × H 10	7	0
E S 32 × A 2	5	0
E S 32 × H 12	4	0
E S 32 × H 10	5	0
E S 34 × E A 37	6	0
E S 34 × E H 14	5	0
E S 36 × E H 28	3	0
E S 36 × H 10	5	0
E S 36 × E A 26	6	0
Total	51	0

The extracted hybrid shorts mated together and also with

Angoras in each case produced a mixture of shorts and Angoras in Mendelian proportions. 10 extracted hybrids mated together and with 2 hybrids of the first generation produced 41 young, of which 31 had short coats and 10 were Angoras; the Mendelian expectation for 40 young is 30 shorts and 10 Angoras. The matings were as follows:—

TABLE 8.

Extracted Hybrids × Hybrids (F_3).

Matings.	*Short.*	*Angora.*
E H 18 × E H 14	2	3
E H 21 × E H 14	5	2
E H 21 × E H 38	5	2
E H 29 × H 10	3	0
E H 29 × E H 27	3	1
E H 31 × H 12	4	0
E H 35 × E H 28	3	1
E H 35 × E H 28	2	0
E H 45 × E H 28	4	1
Total	31	10

7 extracted hybrids mated with 8 Angoras produced 50 young, of which 27 had short coats and 23 were Angoras; the Mendelian expectation is 25 shorts and 25 Angoras. The matings were as follows:—

TABLE 9.

Extracted Hybrids × Angoras (F_3).

Matings.	*Short.*	*Angora.*
E H 17 × A 2	2	3
E H 18 × A 2	2	1
E H 19 × A 2	1	1
E H 21 × A 2	2	2
A 23 × E H 28	2	2
E A 15 × E H 28	3	1
E A 16 × E H 28	1	1
E A 16 × E H 28	4	2
E A 20 × E H 28	2	2
E H 31 × E A 26	3	3
E A 33 × E H 28	2	1
E H 44 × A 24	3	4
Total	27	23

From the above results it would appear that the unit characters, short and Angora coat, in their heredity follow the Mendelian type *Pisum* as regards dominance, segregation, and gametic purity.

(2) NORMALITY AND ALBINISM.

The normal Belgian rabbit has a pigmented skin, coloured coat, dark eyes, and normal demeanour, while the albino Angora has a clear skin devoid of pigment, white coat, pink eyes, and a curious habit of swaying the head from side to side whenever the body is at rest. So far as these experiments go, all these apparently different characters of the albino are correlated and inherited as a single character or unit, which may be simply called albinism as opposed to normality.

In describing these experiments, therefore, it will be understood that the term normal includes a pigmented skin, coloured coat, dark eyes, and normal demeanour, while the term albino comprises a clear skin, white coat, pink eyes, and the swaying habit. As already noted, both the normal Belgians and the albino Angoras breed true when mated with their own kind.

(a) *First Generation* (F_1).

No. 1 normal doe mated with No. 2 albino buck produced 26 normal hybrids. The reverse cross, No. 3 albino doe mated with No. 4 normal buck, produced 16 normal hybrids. The 26 normal hybrids of the first cross did not show the slightest trace of the albino parentage in any respect. The 16 normal hybrids of the reverse cross (with one exception) had a few white markings on the fore extremities, but, as will be seen later, these do not seem to be connected with simple albinism at all, but rather with the Dutch markings latent in the albino (see under Sect. 4, p. 314). In Mendelian terms, therefore, normality may be said to be dominant over albinism, which is recessive.

Further experiments recently carried out show that the normal character of other races as well as the Belgian is similarly dominant over albinism. Altogether 94 hybrids have been raised by crossing normal and albino individuals and all have proved to be normal hybrids, whether the albino was used as the male or the female parent. It appears that in these cases also the phenomenon of dominance is peculiar to the character itself, and is not influenced by change of sex, individuals, or race. The individual matings were as follows. N = normal, A = Albino. No. 47 is a Silver Fawn; Nos. 51 and 52 are Dutch; Nos. 1, 4, 13, and 25 are Belgians; and Nos. 2, 3, 6, 23, and 50 are Angoras.

TABLE 10.

Normal × Albino (F_1).

Matings.	*Normal.*	*Albino.*
N 1 × A 2	26	0
A 3 × N 4	16	0
A 3 × N 51	11	0
A 6 × N 4	8	0
N 13 × A 2	4	0
A 23 × N 25	16	0
A 50 × N 47	8	0
N 52 × A 2	5	0
Total	94	0

(b) *Second Generation* (F_2).

The normal hybrids of the first generation bred together produced a mixture of normals and albinos in Mendelian proportions. 7 normal hybrids bred together produced 171 young, of which 132 were normal and 39 were albinos. The Mendelian expectation for 172 young is 129 normals and 43 albinos.

Each individual hybrid that was tested produced both normals and albinos, usually in the same litter. The individual results were as follows:—No. 5 gave 13 normals and 4 albinos; No. 7, 22 N and 9 A; No. 8, 28 N and 4 A; No. 9, 43 N and 14 A; No. 10, 92 N and 24 A; No. 11, 26 N and 8 A; and No. 12, 40 N and 15 A.

It will be observed that No. 8 gives a decided *deficiency* of albinos, while, as will be seen later, the same individual in a previous litter gave an unexpected *excess* of albinos when mated with an albino.

The albinos of the second generation extracted from the normal hybrids of the first generation had apparently the same albinic characters as the original albino grand-parents, viz., a clear skin devoid of pigment, pure white coat, pink eyes, and the swaying habit.

The normals of the second generation had apparently the same normal characters as the original normal grand-parents and the normal parents, viz., a pigmented skin, coloured coat, dark eyes, and normal demeanour. The majority were self-coloured like the original normals, while some were slightly marked with white on the fore extremities, and a few were marked like the pure Dutch rabbit. As will be seen later, these Dutch markings are apparently not connected with simple albinism (see under Sect. 4, p. 314).

The following table gives the individual matings with the details of each litter :—

Table 11.

Hybrid Normals bred together (F_2).

Matings.	*Normal.*	*Albino.*
H 5 × H 12	6	3
H 5 × H 10	7	1
H 7 × H 10	4	4
H 7 × H 10	3	1
H 7 × H 10	7	2
H 7 × H 12	8	2
H 8 × H 10	8	1
H 8 × H 10	8	1
H 8 × H 10	8	1
H 8 × H 10	4	1
H 9 × H 10	8	0
H 9 × H 10	5	2
H 9 × H 10	6	2
H 9 × H 10	7	1
H 9 × H 10	7	2
H 9 × H 10	4	3
H 9 × H 12	6	4
H 11 × H 12	6	2
H 11 × H 12	7	1
H 11 × H 12	7	3
H 11 × H 10	6	2
Total	132	39

The normal hybrids of the first generation bred back with the original albinos produced a mixture of normals and albinos in Mendelian proportions.

5 normal hybrids mated with 2 albinos produced 54 young, of which 25 were normals and 29 were albinos. The Mendelian

expectation is 27 normals and 27 albinos. Each hybrid tested produced both kinds, usually in the same litter, but, curiously enough, H 8 × A 2 gave in the first litter 5 young *all albinos*, while in the second litter there were 6 normals and 2 albinos, instead of the expected 4 of each. It will be noted that H 8 was the individual which gave a *deficiency* of albinos in the 4 succeeding litters when mated with H 10. The individual matings were as follows:—

TABLE 12.

Hybrid Normals × Albinos (F_2).

Matings.	*Normal.*	*Albino.*
H 5 × A 2	2	2
H 5 × A 2	4	1
H 5 × A 2	3	4
H 7 × A 2	3	4
H 8 × A 2	0	5
H 8 × A 2	6	2
A 3 × H 10	4	2
A 3 × H 10	2	5
A 3 × H 12	1	4
Total	25	29

2 normal hybrids of the first generation mated with one of the original normals produced 20 young, all normals. The matings were N 1 × H 12, producing 11 young in 2 litters, and N 1 × H 10, producing 9 young in 1 litter. The Mendelian expectation is, of course, all normals.

(c) *Third Generation* (F_3).

The albinos of the second generation extracted from the hybrid normals of the first generation bred true when mated with one another and with other albinos, in accordance with the Mendelian expectation. 4 extracted albinos mated together and with 2 other albinos produced 21 young, all of which were albinos. The matings were as follows:—

TABLE 13.

Extracted Albinos × Albinos (F_3).

Matings.	*Normal.*	*Albino.*
E A 16 × A 2	0	5
E A 16 × A 61	0	7
E A 34 × E A 14	0	5
E A 45 × A 61	0	4
Total	0	21

The extracted albinos, like the pure-bred albinos, proved to be recessive to pure normals.

6 extracted albinos mated with 3 pure and 3 extracted normals produced 62 young, all of which were normals, in accordance with the Mendelian expectation.

The individual matings were as follows (E N = Extracted pure normal):—

TABLE 14.

Extracted Albinos × Pure Normals (F_3).

Matings.	*Normal.*	*Albino.*
E A 15 × N 25	6	0
E A 15 × E N 28	4	0
E A 15 × N 51	8	0
E A 16 × E N 28	6	0
E A 16 × E N 28	6	0
E A 34 × N 49	8	0
E A 39 × N 51	2	0
E A 39 × N 51	6	0
E N 43 × E A 14	7	0
E N 44 × E A 14	4	0
E A 45 × E N 28	5	0
Total	62	0

The extracted albinos, like the pure-bred albinos, gave a mixture of normals and albinos in Mendelian proportions when mated with hybrid normals. 5 extracted albinos mated with 6 hybrid normals produced 47 young, of which 23 were normals and 24 were albinos. The Mendelian expectation for 48 young is 24 normals and 24 albinos.

The matings were as follows (EH = Extracted hybrid):—

TABLE 15.

Extracted Albinos × Hybrid Normals (F_3).

Matings.	*Normal.*	*Albino.*
E A 15 × H 12	4	3
E H 18 × E A 14	4	2
E H 19 × E A 14	1	4
E H 19 × E A 14	2	4
E H 21 × E A 38	5	2
E H 21 × E A 14	3	4
E A 34 × E H 37	2	4
E A 39 × E H 41	2	1
Total	23	24

From the above experiments with albinos of the second generation extracted from the normal hybrids of the first generation it is clear that not only are the extracted albinos indistinguishable in their albinism from the pure-bred albinos, but in their breeding they behave precisely as do the pure-bred albinos, viz.:—(1) They breed true with one another; (2) they are recessive to pure normals; (3) they give mixed offspring when mated with hybrid normals. These facts are all in accordance with the Mendelian conception of gametic purity; and there seems to be no doubt that, notwithstanding their hybrid origin, these extracted albinos are pure albinos.

The normal individuals of the second generation, tested with albinos and hybrids, proved to be of two kinds, pure and hybrid; the former producing all normals, and the latter a mixture of normals and albinos. Out of 21 individuals tested, 7 were extracted from hybrids of the first generation mated back with the original albinos (H × A), and these all proved to be hybrids in accordance with the Mendelian expectation. 2 individuals were extracted from 2 hybrids of the first generation mated back with the original normal (H × N), and these have so far proved to be pure normals; the Mendelian expectation for 2 such individuals is 1 pure and 1 hybrid. The remaining 13 individuals were extracted from hybrids of the first generation bred together (H × H), and of these 4 proved to be pure normals and 9 were hybrid normals; the Mendelian expectation for 12 such individuals is 4 pure and 8 hybrids.

The 6 pure extracted normals mated with 4 albinos and 8 hybrids produced 83 young, all normals in accordance with the Mendelian expectation. The individual matings were as follows :—

TABLE 16.

Extracted Normals × Albinos and Hybrids (F_3).

Matings.	*Normal.*	*Albino.*
H 7 × E N 28	7	0
A 23 × E N 28	6	0
E N 32 × A 2	7	0
E N 44 × A 24	7	0
E H 20 × E N 28	6	0
E N 30 × H 10	5	0
E N 30 × H 10	7	0
E N 32 × H 12	5	0
E N 32 × H 10	5	0
E N 32 × H 10	6	0
E H 33 × E N 28	6	0
E N 35 × E H 26	6	0
E H 36 × E N 28	3	0
E N 43 × E A 14	7	0
Total	83	0

The extracted hybrid normals mated together, and also with albinos, in each case produced a mixture of normals and albinos in Mendelian proportions. 10 extracted hybrids mated together and with 2 hybrids of the first generation produced 55 young, of which 38 were normals and 17 were albinos; the Mendelian expectation for 56 young is 42 normals and 14 albinos. The excess of albinos appears to be due to the peculiarity of E H 26, which gave 11 normals and 9 albinos instead of the expected 15 and 5. The individual matings were as follows:—

TABLE 17.

Extracted Hybrids × Hybrids (F_3).

Matings.	*Normal.*	*Albino.*
E H 29 × H 10	5	2
E H 29 × E H 27	5	1
E H 31 × H 12	3	1
E H 31 × E H 26	3	3
E H 36 × H 10	4	1
E H 36 × E H 26	4	4
E H 42 × E H 26	4	2
E H 53 × E H 37	6	1
E H 54 × E H 41	4	2
Total	38	17

8 extracted hybrids mated with 5 albinos produced 89 young, of which 44 were normals and 45 were albinos; the Mendelian expectation for 90 young is 45 normals and 45 albinos. The individual matings were as follows:—

TABLE 18.

Extracted Hybrids × Albinos (F_3).

Matings.	*Normal.*	*Albino.*
E H 17 × A 2	2	1
E H 17 × A 2	5	3
E H 18 × A 2	2	3
E H 18 × A 2	2	3
E H 18 × A 2	1	3
E H 18 × E A 14	4	2
E H 18 × A 2	4	1
E H 19 × A 2	2	3
E H 19 × E A 14	1	4
E H 19 × E A 14	2	4
E H 20 × A 2	3	1
E H 21 × A 2	4	0
E H 21 × A 2	2	3
E H 21 × E A 14	3	4
E H 33 × A 24	3	5
E A 34 × E H 37	2	4
E A 39 × E H 41	2	1
Total	44	45

From the above results it would appear that the unit characters normality and albinism in their heredity also follow the Mendelian type *Pisum* as regards dominance, segregation, and gametic purity.

(3) COAT COLOUR.

The grey coat of the common wild rabbit is made up for the most part of yellow hairs based and tipped with black. The extent of the coloured portions is somewhat variable in individual hairs; generally, however, the black basal portion is more extensive than the yellow middle portion, while the black apical tip is less. In these parti-coloured hairs both the yellow and black pigments occur in different dilutions. Thus, in the patch of short fluffy hairs behind the ears the yellow portion of each hair is a bright tan-yellow; while along the back, towards the tail and down the flanks on each side, the yellow becomes more diluted, passing from tan through fawn, buff, and cream to white under the tail and belly, where the yellow pigment is not evident. In the same way the black portions of the hairs, both basal and apical, become diluted, passing from dense black through blue-black, slate-grey, and grey-white to white.

This dilution of the black pigment is especially noteworthy in the roots of the hairs, giving the impression of a blue-black ground-colour close to the skin, when the hairs are blown aside. A certain amount of chocolate or brown pigment appears to be always associated with the black.

Amongst the parti-coloured yellow and black hairs which go to form the grey coat there are a few long black hairs scattered more or less regularly, especially along the back and loins and on the ears and forehead. These long black hairs give a wavy appearance to the coat, known to fanciers as "ticking"; they are more or less shaded with brown, have blue-black roots, and do not usually appear until about the age of two months.

The above observations show that the hairs which make up the grey coat of the wild rabbit contain at least two distinct pigments—yellow and black, with their dilutions; and most probably a third, brown or chocolate, which is more or less evident in close association with the black pigment. (*Cf.* Mr. Bateson's, Miss Durham's, and Dr. Allen's observations on similar pigments in Mice: Bateson, 1903; Allen, 1904.)

The yellow-grey coat of the Belgian rabbit used in these experiments contains the same pigments, and is in all respects similar in nature to that of the wild grey, except that it contains a larger proportion of yellow pigment and less black in the individual parti-coloured hairs in all parts of the coat. This increase of yellow and reduction of black appears to affect the basal part of the hairs more than the tips.

Further, the bright tan-yellow, which is usually confined to the space behind the ears in the wild grey, is extended to the chest and flanks in the yellow-grey, though this also shades off, downward and backward, through fawn, buff, and cream, to white, as in the wild grey. The creamy-white hairs borne underneath in the wild grey have blue-black roots, giving them a grey-white appearance; while those of the yellow-grey in the same place have apparently no trace of the diluted black pigment, being almost pure white. The long black hairs also appear to be less in number in the yellow-grey than in the wild grey, and do not extend so far down the flanks. In all respects, therefore, the yellow-grey has more yellow and less black pigment than the wild grey.

The yellow-grey type breeds perfectly true to the above colour-details, and can always be distinguished from the wild grey.

The coat of the albino Angora is of course pure white, with no trace of any kind of pigment.

(a) *First Generation* (F_1).

The yellow-grey Belgians crossed with the white Angoras gave hybrids all of which had wild-grey coats, no matter which way the cross was made.

No. 1 yellow-grey doe mated with No. 2 white buck produced 26 young with coats indistinguishable from those of the wild grey. In the reverse cross, No. 3 white doe mated with No. 4 yellow-grey buck, gave 16 young, all with wild-grey coats. One individual (No. 7) from the latter mating had, when young, rather more yellow on the chest and flanks than the others; but after the second moult it became almost wild grey, like the rest. Further experiments recently carried out have given similar results: altogether 70 individuals have been raised by mating yellow-grey with white, and all have wild-grey coats. The following table gives the results of the individual matings (Y G=yellow-grey, W=white):—

Table 19.

Yellow-grey × White (F_1).

Matings.	*Wild Grey.*
Y G 1 × W 2	26
W 3 × Y G 4	16
W 6 × Y G 4	8
Y G 13 × W 2	4
W 23 × Y G 25	16
Total	70

(b) *Second Generation* (F_2).

The greys of the first generation bred together, with one exception, proved to be hybrid greys containing recessive black, giving a mixture of greys and blacks, the exception giving all greys. 7 greys of the first generation were tested together, and of these 6 proved to be hybrids, giving both grey and black young, usually in the same litter: the remaining one has so far given no blacks, and presumably is a pure grey.

The pure grey doe (No. 7) mated with 2 hybrid greys containing latent black (Nos. 10 and 12) produced 22 grey young.

The 6 hybrid greys mated together produced 110 coloured young, of which 85 were greys and 25 were blacks.

The individual results were as follows:—No. 5 gave 8 greys and 5 blacks; No. 8, 22 G and 6 B; No. 9, 33 G and 10 B; No. 10, 59 G and 19 B; No. 11, 22 G and 4 B; and No. 12, 26 G and 6 B.

All the 7 individuals gave white as well as coloured offspring; but these have already been dealt with under albinism (Sect. 2, p. 294).

The following table gives the individual matings, with the numbers of greys and blacks in each litter:—

TABLE 20.

Hybrid Greys bred together (F_2).

Matings.	*Grey.*	*Black.*
H 5 × H 12	4	2
H 5 × H 10	4	3
H 8 × H 10	5	3
H 8 × H 10	8	0
H 8 × H 10	6	2
H 8 × H 10	3	1
H 9 × H 10	5	3
H 9 × H 10	5	0
H 9 × H 10	5	1
H 9 × H 10	7	0
H 9 × H 10	2	5
H 9 × H 10	3	1
H 9 × H 12	6	0
H 11 × H 12	5	1
H 11 × H 12	6	1
H 11 × H 12	5	2
H 11 × H 10	6	0
Total	85	25

The greys of the second generation had wild-grey coats like their parents, a few individuals appeared to have rather more yellow and less black than the wild grey; but, curiously enough, not one was a true yellow-grey like the Belgian grand-parent. The blacks of the second generation had black coats with no trace of the yellow pigment of the grey parents; all appeared to be shaded more or less with the brown pigment which is always associated with black, especially when the coat is moulting.

The nest coat was jet-black, but, in common with other black rabbits, after the first moult a few white hairs appeared, chiefly on the back and loins; these apparently increase in number with each moult, and a few have already developed these white hairs to such an extent as to almost resemble the well-known "Silver Grey" breed of the fanciers ("Chinchilla" of Darwin). It is hardly necessary to say that the so-called "Silver Grey" has no resemblance whatever to the wild grey, being a pure black breed when young; afterwards a number of white hairs appear among the black, giving it that silvered appearance so much admired by fanciers. The black individuals were easily distinguished from the grey ones at birth, their pigmented skin being a shade darker and covering the whole body, unlike the greys, in which the ventral area is but little pigmented, being pink or flesh-coloured.

The hybrid greys of the first generation, mated back with one of the original whites, also gave a mixture of greys and blacks, but only a few were raised.

The matings were as follows:—H 5 × W 2 gave 6 greys and 3 blacks, and H 8 × W 2 gave 5 greys and 1 black.

(c) *Third Generation* (F_3).

The blacks of the second generation extracted from the hybrid greys of the first generation have, so far, bred true when mated with one another[*]. 5 individuals tested together gave 16 young, all blacks with no trace of yellow pigment. The following were the matings: E B 20 × E B 28 gave 6 blacks; E B 33 × E B 28 gave 6 blacks; and E B 54 × E B 41 gave 4 blacks. (For further results showing the purity of the extracted blacks, see Table 22.)

One of the extracted blacks E B 28 was mated with the pure grey G 7, producing 7 grey young.

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[*] Excluding the albinos thrown, which have been already dealt with under Sect. 2, p. 298.

The same extracted black was also mated with a hybrid grey E H 35, producing 2 greys and 5 blacks.

The greys of the second generation have, so far as tested, proved to be of two kinds, pure and hybrid, the former giving all greys, and the latter a mixture of greys and blacks. Out of 9 greys tested, 8 have proved to be hybrids containing recessive black, each of the 8 gave a mixture of greys and blacks, and in all there were 48 young, of which 38 were greys and 10 were blacks.

The matings were as follows:—

TABLE 21.

Hybrid Greys bred together (F_3).

Matings.	*Grey.*	*Black.*
E H 29 × H 10	4	1
E H 29 × E H 27	4	1
E H 30 × H 10	4	1
E H 30 × H 10	5	2
E H 31 × H 12	2	1
E H 31 × E H 26	3	0
E H 32 × H 12	5	0
E H 32 × H 10	4	1
E H 35 × E H 26	5	1
E H 42 × E H 26	2	2
Total	38	10

The remaining grey has, so far as tested, proved to be a pure grey, giving 11 grey young when mated with a black and with 2 hybrid greys. The matings were:—E G 36 × E B 28 giving 3 greys; E G 36 × H 10 giving 4 greys; and E G 36 × E H 26 giving 4 greys. As these numbers are few, it is possible that this individual may yet prove to be a hybrid grey containing recessive black, and further experiments are necessary before we can be quite sure that it is a pure grey, especially as all the other 8 greys tested proved to be hybrids.

Both the greys and blacks of the third generation had similar coats to those of the second generation, there being still no return to the original yellow-grey of the Belgian.

Summary of Coat-Colour Results.

In the first generation (F_1) yellow-grey × white gave all wild greys. In the second generation (F_2), with one exception, the F_1 greys proved to be hybrids containing recessive black, for, when bred together, they gave a mixture of greys and blacks in Mendelian proportions. In the third generation (F_3) the F_2 blacks have so far bred true when mated together; they are recessive to pure grey and give a mixture of greys and blacks when mated with hybrid greys. The F_2 greys so far appear to be of two kinds, pure and hybrid, and the hybrids bred together give a mixture of greys and blacks in Mendelian proportions. From the Mendelian point of view the above results are what might have been expected had the original parents been grey × black instead of yellow-grey × white.

Two points therefore appear to demand consideration:—The appearance of the black character, and the disappearance of the yellow-grey character.

The Appearance of the Black Character.

The sudden appearance of the black character in the second generation was quite unexpected, as there had been no black individuals in the ancestry of either of the original parents—Belgian or Angora—for at least 8 generations and probably many more. The fact that these black individuals appeared in about the proportion of one quarter and bred true at once was very significant from the Mendelian point of view. It suggested that the hybrid greys of the first generation were giving off gametes, one half of which contained the factor for black coat-colour. As these hybrid greys were bred from the yellow-grey Belgians crossed with the white Angora, it appeared that the black factor must have been introduced by one or the other of these parents, or by both.

That it was not introduced by both is clear from the absence of blacks in the first generation. That it was not introduced by the Belgian is equally clear from the fact that no blacks appeared when the Belgian was mated with a pure black, nor when the Belgians were mated together. From the Mendelian point of view, therefore, it would appear that the black factor must have been introduced by the white Angora. This may appear incredible, and yet, as the following experiments show, it seems to be the only interpretation of the facts.

*Colour-factors latent * in Pure-bred Albinos.*

The 2 albino Angoras originally used in the experiments were tested by mating them with the pure blacks of the second generation. No. 2 albino buck mated with 4 black does gave 16 black young. No. 3 albino doe mated with a black buck gave 11 young, of which 5 were black and 6 were grey. These results are in accordance with the conception that No. 2 albino gave off gametes, all of which carried the black factor, while No. 3 albino gave off gametes, some of which carried the black factor and others the grey factor.

To test the matter still further, No. 2 albino was mated with 5 grey hybrids known to contain recessive black, producing 38 coloured young, of which 21 were greys and 17 were blacks. If, as conceived, No. 2 albino was carrying latent black simply, the Mendelian expectation in this mating is 19 greys and 19 blacks. Again, No. 3 albino was mated with 2 grey hybrids known to contain recessive black, producing 7 coloured young, of which 5 were greys and 2 were blacks. These numbers are few, but if, as conceived, No. 3 albino was carrying both latent grey and latent black factors, the Mendelian expectation for 8 young is 6 greys and 2 blacks. This conception also explains certain facts in regard to the gametic constitution of the individuals of the first generation which are otherwise obscure. It will be remembered that while all the greys of the first generation by the No. 2 albino were hybrids containing recessive black, yet one individual grey (No. 7) out of No. 3 albino was a pure grey containing no black. The above conception that No. 2 albino gave off all black gametes, while No. 3 albino gave off both grey gametes and black gametes would explain the above facts, which were previously obscure.

In order to test whether these latent factors in albinos were subject to Mendelian segregation in simple albino matings, the No. 3 albino doe, apparently carrying grey and black, was mated with No. 2 albino buck, apparently carrying black only. 14 young were produced, all albinos, of course, with no trace of pigment. 2 of these young were tested with pure blacks and have so far given the following results :—

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* To prevent misconception it should be stated that the colour-factors present in albinos are "*latent*" in the sense that their influence is not evident until some other ingredient, found in a pigmented individual, is added to them. When the precise nature of pigmentation is determined, it may be possible to substitute a more precise term. (*Cf.* Cuénot, 1903.)

No. 23 albino doe mated with a pure black gave 5 blacks and 1 grey. No. 24 albino buck mated with a pure black gave 3 blacks: mated with a grey hybrid containing recessive black gave 6 blacks and 1 grey.

Although these results are few in number, yet it seems certain that No. 23 albino is carrying both grey and black, while No. 24 is apparently carrying black only.

The Mendelian expectation for albino (gr.-bl.) × albino (bl.) is 1 albino (gr.-bl.) and 1 albino (bl.), which is apparently the result. The fact that in this case father and son are apparently carrying black only, while mother and daughter are apparently carrying grey and black, may be but a coincidence.

All the above results with pure-bred albinos are in accordance with the conception that albinos give off gametes carrying certain colour-factors which remain latent until the albino is crossed with a pigmented individual, and yet, during their latency, obey the Mendelian laws of segregation and gametic purity. Further support is given to this conception by the results of the following experiments with extracted albinos.

Colour-factors latent in Extracted Albinos.

7 extracted albinos were tested for latent colour-factors, and of these, 2 apparently carried black only, while 5 apparently carried both grey and black. No. 14 albino buck mated with 2 pure blacks gave 6 blacks : mated with 2 grey hybrids containing recessive black it gave 3 greys and 5 blacks.

No. 45 albino doe mated with two pure blacks gave 9 blacks. These two albinos, which were apparently carrying black only, were extracted from No. 5 grey hybrid containing black, mated with No. 2 albino apparently carrying black, and are interesting as showing that albinos apparently carrying black only can be extracted from greys provided that the latter also contain black. No. 15 albino doe mated with 2 pure blacks gave 5 greys and 7 blacks ; this albino was extracted out of No. 8 grey (bl.) × No. 2 albino (bl.).

No. 16 albino doe mated with a pure black gave 7 greys and 5 blacks; this albino was extracted out of No. 7 pure grey × No. 2 albino (bl.).

This case is interesting as showing that an albino extracted out of a pure grey does not necessarily carry grey only, the result depends upon both parents.

No. 34 albino doe mated with a pure black gave 4 greys and 4 blacks; this albino was extracted out of No. 11 grey (bl.) × No. 12 grey (bl.).

No. 38 albino buck mated with a pure black gave 3 greys and 2 blacks.

No. 39 albino doe mated with two pure blacks gave 6 greys and 4 blacks.

The last two albinos were extracted from No. 7 pure grey × No. 10 grey (bl.).

The three following tables give the individual matings in the testing of the pure-bred and extracted albinos for their latent colour-factors.

4 albinos apparently carrying black only mated with 7 pure blacks gave 34 black young, in accordance with the Mendelian expectation. These 34 blacks may therefore be added to the 16 already recorded under extracted blacks bred together (p. 303) making 50 in all, and will serve as a further illustration of the purity of the black recessives.

TABLE 22.

Albino (black) × Black.

Matings.	*Grey.*	*Black.*
E B 19 × A 2	0	2
E B 19 × E A 14	0	3
E B 20 × A 2	0	3
E B 21 × A 2	0	4
E B 21 × A 2	0	2
E B 21 × E A 14	0	3
E B 33 × A 24	0	3
E A 45 × E B 28	0	5
E A 45 × B 61	0	4
B 52 × A 2	0	5
Total	0	34

7 albinos apparently carrying both grey and black mated with 5 pure blacks gave 64 young, of which 32 were greys and 32 were blacks, which is exactly the Mendelian expectation.

Table 23.

Albinos (grey and black) × Black.

Matings.	*Grey.*	*Black.*
A 3 × B 51	3	3
A 3 × B 51	3	2
A 23 × E B 28	1	5
E A 15 × E B 28	2	2
E A 15 × B 51	3	5
E A 16 × E B 28	3	3
E A 16 × E B 28	4	2
E A 34 × B 49	4	4
E B 21 × E A 38	3	2
E A 39 × E B 41	2	0
E A 39 × B 51	0	2
E A 39 × B 51	4	2
Total	32	32

3 albinos, apparently carrying black only, mated with 6 grey hybrids containing black, gave 53 young, of which 25 were grey and 28 were black; the Mendelian expectation for 54 young being 27 greys and 27 blacks.

The results of the last table and this may also be added to the results given previously under hybrid greys mated with extracted blacks, giving in all 124 young, of which 59 were greys and 65 were blacks. The Mendelian expectation is 62 greys and 62 blacks (see p. 303).

Table 24.

Albino (black) × Grey (black).

Matings.	*Grey.*	*Black.*
H 5 × A 2	2	0
H 5 × A 2	1	3
H 5 × A 2	3	0
H 8 × A 2	5	1
E H 17 × A 2	2	0
E H 17 × A 2	1	4
E H 18 × A 2	0	2
E H 18 × A 2	0	2
E H 18 × A 2	0	1
E H 18 × A 2	3	1
E H 18 × E A 14	1	3
E H 32 × A 2	4	3
E H 44 × E A 14	2	2
E H 44 × A 24	1	6
Total	25	28

The above results point to the following conclusions:—

(1) That both pure-bred and extracted albinos carry in their gametes certain colour-factors.

(2) Some albinos give off gametes containing the black factor only, while others give off gametes containing black and gametes containing grey, on the average in equal numbers.

(3) These colour-factors remain latent when albinos are mated together, but become patent when the albinos are mated with normal individuals.

(4) These latent colour-factors appear to follow the ordinary Mendelian rules of segregation and gametic purity.

(5) That the black character, which appeared in the second generation of the hybrids between the yellow-grey Belgian and the white Angora, was introduced by the albino Angora.

These conclusions, arrived at from experiments with Rabbits, fully confirm those already obtained by Prof. Cuénot in his important experiments with Mice; and although of necessity my experiments have been carried out on somewhat different lines, yet the conclusions are the same in principle, and in presenting them I wish to acknowledge my indebtedness to Prof. Cuénot and Mr. Bateson for their useful suggestions. There is no doubt that the demonstration of the fact of latent colour-factors being carried by albinos is of great significance, and will help to throw light upon a large number of observations, contributed by many observers in both animals and plants, that hitherto have remained obscure.

The Disappearance of the Yellow-grey Character.

With regard to the disappearance of the original yellow-grey character of the Belgian in all the generations, a number of experiments are now in progress, which, it is hoped, will throw some light upon the matter as soon as completed *.

(4) UNIFORM AND MARKED COAT.

In the original experiments the Belgian parents had a uniform or self-coloured coat, with no trace of white markings on the extremities. (The almost white ventral area may for this purpose be disregarded.)

This self-colour character breeds true, so far as my experiments go, and to my knowledge for at least 8 previous generations and probably many more.

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* So far it is not possible to suggest what is the meaning of the non appearance of the Belgian coat-colour in F_2 and F_3.

The 2 pure self-coloured Belgians were mated with 2 albino Angoras, and each albino gave a different result.

No. 2 albino buck mated with No. 1 self-coloured doe produced 26 self-coloured young with no trace of white markings on the extremities.

No. 3 albino doe mated with No. 4 self-coloured buck produced 16 young, of which one only was self-coloured, all the others being more or less marked with white on the fore-feet, shoulders, breast, nose, and forehead.

These white markings, though variable in extent, increased in a definite direction. The slightest markings were either on the tip of a fore-paw or at the end of the nose; as the markings increased they invaded the whole fore-feet, legs, shoulders, and breast, while the nose-markings extended towards the forehead; in other words, the whole tendency of the markings was towards the Dutch markings, so well known to fanciers. No. 7 was self-coloured, while No. 10 had white fore-feet, legs, right shoulder, and breast, being the most marked of all; the others might be said to consist of a series between Nos. 7 and 10.

As different results were obtained from the 2 albinos, it is necessary to consider the offspring of the 2 lines of descent separately, viz. :—The self-coloured line raised from the No. 2 albino, and the marked line raised from the No. 3 albino.

(a) *The Self-coloured Line.*

In the first generation all the offspring were self-coloured. In the second generation 3 of the selfs of the first generation bred together and with a pure self produced 37 young, of which 35 were selfs and 2 were slightly marked with white, having a few white hairs on the tip of the right paw. The matings were as follows:—

TABLE 25.

Self × Self (F_2).

Matings.	*Self.*	*Marked.*
S 1 × S 12	11	0
S 5 × S 12	5	1
S 11 × S 12	19	1
Total	35	2

In the third generation 5 of the selfs of the second generation mated together and with 2 pure selfs produced 25 young, all self-coloured. The matings were as follows:—

TABLE 26.

Self × Self (F_3).

Matings.	*Self.*	*Marked.*
S 31 × S 12	3	0
S 31 × S 26	3	0
S 32 × S 12	5	0
S 42 × S 26	4	0
S 43 × S 25	10	0
Total	25	0

In the self-coloured line therefore, with two slight exceptions, the selfs bred true for three generations, including 88 individuals, notwithstanding that all were originally bred from an albino.

(b) *The Marked Line.*

In the first generation all the offspring, except one, were more or less marked with white on the fore extremities. In the second generation, 4 of the individuals of the first generation bred together produced 67 young, of which 16 were selfs, 34 were slightly marked with white like the parents, and 17 had the true Dutch markings. The individual numbers were as follows:—No. 7 gave 5 selfs, 2 marked, and 6 Dutch; No. 8 gave 3 selfs, 9 marked, and 6 Dutch; No. 9 gave 8 selfs, 23 marked, and 5 Dutch. It will be noted that each individual gave all three kinds; that No. 7, the self-coloured exception, gave more than the average number of full Dutch-marked and also of selfs; that No. 9, the one most marked with white, gave less than the average number of Dutch-marked. The individual matings and details of each litter were as follows (S=self-coloured hybrid, M=marked hybrid):—

TABLE 27.

Hybrid Self and Marked × Marked (F_2).

Matings.	*Self.*	*Marked.*	*Dutch.*
S 7 × M 10	1	1	1
S 7 × M 10	2	0	1
S 7 × M 10	2	1	4
M 8 × M 10	0	4	4
M 8 × M 10	2	4	2
M 8 × M 10	1	1	0
M 9 × M 10	2	6	0
M 9 × M 10	1	4	0
M 9 × M 10	0	4	2
M 9 × M 10	2	4	1
M 9 × M 10	1	4	1
M 9 × M 10	2	1	1
Total	16	34	17

In the third generation, 3 of the extracted selfs bred together and with a pure self produced 15 young, of which 14 were selfs and 1 was slightly marked with white on the tip of the left paw. The matings were as follows :—

TABLE 28.

Extracted Selfs × Selfs (F_3).

Matings.	*Self.*	*Marked.*	*Dutch.*
E S 35 × E S 26	6	0	0
E S 36 × E S 26	3	1	0
E S 36 × S 47	5	0	0
Total	14	1	0

4 of the extracted Dutch bred together have so far given 10 young, all Dutch-marked. The matings were :—E D 53 × E D 37 gave 6 Dutch, and E D 54 × E D 41 gave 4 Dutch. 3 of the extracted marked individuals bred together and with hybrids gave 17 young, of which 3 were selfs, 12 were marked, and 2 were Dutch. The matings were :—E M 29 × M 10 gave 0 selfs, 4 marked, and 1 Dutch ; E M 29 × E M 27 gave 1 self, 3 marked, and 1 Dutch ; S 7 × E M 28 gave 2 selfs, 5 marked, and 0 Dutch.

The Appearance of the Dutch Markings.

The appearance of the true Dutch markings in the second generation of the marked line only was as interesting as it was unexpected, especially as there had been no Dutch-marked individual in the ancestry of either the original self-coloured Belgian or the white Angora for at least 8 generations, and probably many more. The fact that these Dutch-marked individuals appeared in about the proportion of one quarter, and bred true at once, was very significant. From the Mendelian point of view, the results pointed to the conclusion that No. 3 albino Angora gave off gametes carrying the factor for Dutch markings, and that these gametes, uniting with the pure self gametes of No. 4 self-coloured Belgian, gave rise to the slightly marked hybrids of the first generation. Ordinary Mendelian segregation apparently took place in the gametes of these intermediate hybrids, giving rise to gametes for self-colour and gametes for Dutch markings in about equal numbers, with the result that in the second generation there were one quarter pure self, one half hybrid marked, and one quarter pure Dutch. In order to test this conception experimentally, a pure self-coloured doe (No. 46) was mated with a pure Dutch buck (No. 51), giving 5 young all slightly marked with white, like the marked hybrids of the first generation between the original albino No. 3 and the self-coloured No. 4.

No. 3 albino was then mated with the same pure Dutch buck (No. 51), giving 11 young, all of which had the true Dutch markings; showing that this albino was indeed giving off gametes, carrying the factor for Dutch markings only.

The other albino No. 2 (which mated with the self-coloured No. 1 gave the self line) was mated with a pure Dutch-marked doe (No. 52, bred out of the same litter as No. 51), giving 5 young, all slightly marked with white, and none with the full Dutch markings; showing that this albino was giving off gametes carrying the factor for self-colour only.

The above results go to show that pure-bred albinos carry the latent factors for self-colour and for Dutch markings.

The extracted albinos were also tested to some extent; and, so far as the experiments go, it appears that they also carry the latent factors for self-colour and Dutch markings.

Thus in the self line, 3 extracted albinos, Nos. 14, 34, and 45, so far as tested, appear to carry the self factor only, for mated with pure selfs they gave 16 young, all selfs, and mated with pure Dutch they gave 6 young, all slightly marked.

In the marked line, No. 39, extracted albino, appears to carry the self factor only, for mated with a pure Dutch it gave 10 young, all slightly marked; while the 2 extracted albinos, Nos. 15 and 16, appear to carry both the self and Dutch factors, for mated with pure selfs they gave 7 selfs and 3 slightly marked, and mated with pure Dutch they gave 10 Dutch and 9 marked.

So far as they go, therefore, the above results point to the following conclusions:—

(1) That both pure-bred and extracted albinos may carry the factors for self-colour and Dutch markings.

(2) Some of the albinos carry the self factor, others the Dutch factor only, and others, again, both the self and Dutch factors.

(3) The factors for coat-pattern remain latent when albinos are mated together, but become patent when the albinos are mated with normal individuals.

(4) The coat-pattern characters—unlike the previous characters dealt with—are neither dominant nor recessive towards one another, but when crossed give intermediate hybrids in the first generation. In the second and third generations, however, these characters appear to follow the ordinary Mendelian rules of segregation and gametic purity.

(5) The Dutch markings, which made their appearance in the second generation of the Belgian-Angora cross, appear to have been introduced by one of the albino Angoras (No. 3) and not the other (No. 2).

(6) The Dutch-marked rabbit would appear, therefore, to be a distinct mutation, rather than a partial albino caused by imperfect segregation. Similarly, the slightly marked forms are to be regarded as variable hybrids between the Dutch-marked and the self-coloured, rather than the result of varying imperfections of segregation from albinism.

These conclusions, arrived at from experiments with Rabbits, in some respects appear to be similar to those already obtained by Prof. Cuénot with Mice, while in other respects they seem to differ. Both results are in agreement so far, that the "panachure" in mice and the Dutch markings in rabbits are unit characters in heredity following the ordinary Mendelian rules of segregation and gametic purity. Both agree, too, in the conclusion that these factors appear to be carried by albinos in a latent state.

The "panachure" in mice, however, seems to differ from the Dutch markings in rabbits, in so far that it appears to be completely recessive to self-colour or uniform coat; while, on the other hand, the Dutch markings, so far as observed, are neither recessive nor dominant to self-colour, giving variable hybrids, the majority of which have white markings tending towards Dutch markings. Occasionally, however, self-coloured hybrids appear, but, so far, no true Dutch-marked.

Another apparent difference between the "panachure" in mice and the Dutch markings in rabbits is that the latter seem to be more definite in character, with the pigment more localized than in the variable spotted mice. Further experiments with Dutch rabbits are now in progress in order to work out, if possible, some of these interesting details.

As will be seen from the list of references, the literature relating to the heredity of coat-colour in mice has been very extensive during the past two years, and space will not allow any detailed references to the important experiments of Cuénot, Darbishire, and Allen, and the valuable work of Bateson and Castle in the Mendelian interpretation of present and past records. Judging from my experience with rabbits, I am inclined to think that most, if not all, of the various complications and difficulties met with in the various experiments with mice may be interpreted by means of the simple Mendelian principles (bearing in mind the important results gained by Cuénot, in regard to the carrying of latent factors by albinos) without recourse to such interesting though complicated conceptions as mosaic gametes and resolution of compound characters.

SUMMARY.

Experiments in crossing Belgian rabbits with albino Angoras, and the subsequent interbreeding of the hybrids, have demonstrated the existence of 4 pairs of unit characters, viz.:—(1) Short and Angora coat; (2) Normality and albinism; (3) Grey and black coat; (4) Self-colour and Dutch markings. Each of these pairs is inherited independently of the other, so that all kinds of combinations occur among the offspring (see Table 29, p. 320).

The first two pairs of unit characters, short and Angora coat, normality and albinism, have been fully investigated, and in their heredity are found to follow Mendel's original *Pisum* type in regard to dominance, segregation, and gametic purity.

Short and Angora coat.—The Angora coat is recessive to short coat in the first generation, segregates in Mendelian proportions in the second generation, and breeds true in the third generation, notwithstanding its dominant short-coated ancestry.

The short coat is dominant over Angora coat in the first generation, and segregates in Mendelian proportions into two breeding forms in the second generation—pure and hybrid.

The pure form breeds true in the third generation, notwithstanding its Angora ancestry, while the hybrid form gives a mixture of shorts and Angoras in Mendelian proportions. Owing to dominance, the pure and hybrid shorts are indistinguishable in appearance, and can only be determined definitely by experimental breeding.

Normality and Albinism.—Albinism is recessive to normality in the first generation, segregates in Mendelian proportions in the second generation, and breeds true in the third generation, notwithstanding its dominant normal ancestry.

Normality is dominant over albinism in the first generation, and segregates in Mendelian proportions into two breeding forms in the second generation—pure and hybrid.

The pure form breeds true in the third generation, notwithstanding its albino ancestry, while the hybrid form gives a mixture of normals and albinos in Mendelian proportions. Owing to dominance, the pure and hybrid normals are indistinguishable in appearance, and can only be determined definitely by experimental breeding.

The investigation of the two remaining pairs of unit characters, grey and black coat, self-colour and Dutch markings, is not yet completed. So far as the experiments go, however, the following results appear:—

Grey and black coat.—Black is recessive to grey in the first generation, segregates in Mendelian proportions in the second generation, and breeds true in the third generation, notwithstanding its grey ancestry.

Grey is dominant over black in the first generation, and appears to segregate into two breeding forms in the second generation—pure and hybrid.

The apparently pure grey has so far bred true in the third generation, but the numbers are not yet sufficient to test the matter definitely. The hybrid greys give a mixture of greys and blacks in Mendelian proportions. Owing to dominance, the pure and hybrid greys are indistinguishable in appearance, and can only be determined definitely by experimental breeding.

In regard to the greys, an interesting complication was observed. The original grey used was a pure yellow-grey, containing more yellow pigment and less black than the ordinary wild grey. The greys of the first, second, and third generations were all wild greys, and, so far, there has been no return to the original pure yellow-grey.

Self-colour and Dutch markings.—So far as the experiments go, these characters appear to be neither dominant nor recessive to one another, but give variable intermediate marked hybrids in the first generation. Segregation into the three forms in Mendelian proportions, however, takes place in the second generation, and, so far, the extracted self-coloured and Dutch-marked forms have bred true in the third generation, while the intermediate marked hybrids give the three forms again in accordance with the Mendelian principles.

Latent factors in Albinos.—With regard to simple albinism, albinos of any ancestry so far breed true, the factor for normality being apparently eliminated in accordance with the Mendelian principles.

With regard to characters other than albinism, *but compatible with it*, such as short and Angora coat, these are carried by albinos in either a patent or recessive state. With regard to characters other than albinism, *but incompatible with it*, such as grey and black coat, self-colour and Dutch markings, these are also apparently carried by albinos, but in a latent state only.

Grey and black coat.—Albinos of the same ancestry extracted from hybrid greys, containing recessive black, so far appear to be of two kinds, viz. :—albinos carrying black, and albinos carrying grey and black.

Pure-bred albinos, with all albino ancestors for at least eight generations, and probably many more, so far appear to be of the same two kinds.

Experiments have not yet been carried out to test whether certain albinos carry grey only.

Self-colour and Dutch markings.—Albinos extracted from self-coloured parents appear to carry the latent factor for self-colour only, while albinos extracted from marked hybrids containing the self and Dutch factors appear to be of two kinds, viz. :—albinos carrying self-colour, and albinos carrying self and Dutch.

Experiments have not yet been carried out to test whether extracted albinos carry Dutch only.

Pure-bred albinos with all albino ancestors for at least eight generations, and probably many more, so far appear to be of the three kinds, viz. :—albinos carrying self only, albinos carrying Dutch only, and albinos carrying both self and Dutch. All these latent factors for coat-colour and coat-pattern apparently carried by albinos do not become patent until the albino is bred with a normal or coloured form, presumably because they are incompatible with albinism. Nevertheless, in their latency, they appear to segregate gametically in albino matings as in normal matings, following the ordinary Mendelian rules of segregation and gametic purity.

These results confirm, and extend to rabbits, results already obtained by Prof. Cuénot in mice, though it would appear that the heredity of Dutch markings in rabbits differs in some respects from that of the "panachure" in mice.

Mendelian Analysis of individual Rabbits used in the Experiments.

The following table gives a list of 45 individual rabbits that have been analysed in these experiments in accordance with the Mendelian principles. First is given the Stud No. of the individual, the sex, the parentage, and the somatic characters somewhat abbreviated. Underneath is given the gametic constitution of the individual as determined in these experiments, the gametic factors being expressed in the same terms as the somatic characters above.

Table 29.

No. 1. ♀ (Pure Belgian) : Short, normal, grey, self.
Gametes : *Short, normal, grey, self.*

No. 2. ♂ (Pure Angora) : Angora, albino, white.
Gametes : *Angora, albino, black, self.*

No. 3. ♀ (Pure Angora) : Angora, albino, white.
Gametes : *Angora, albino, grey & black, Dutch.*

No. 4. ♂ (Pure Belgian) : Short, normal, grey, self.
Gametes : *Short, normal, grey, self.*

No. 5. ♀ (1 × 2) : Short, normal, grey, self.
Gametes : *Short & Angora, normal & albino, grey & black, self.*

No. 7. ♀ (3 × 4) : Short, normal, grey, self.
Gametes : *Short & Angora, normal & albino, grey, self & Dutch.*

No. 8. ♀ (3 × 4) : Short, normal, grey, marked.
Gametes : *Short & Angora, normal & albino, grey & black, self & Dutch.*

No. 9. ♀ (3 × 4) : Short, normal, grey, marked.
Gametes : *Short & Angora, normal & albino, grey & black, self & Dutch.*

No. 10. ♂ (3 × 4) : Short, normal, grey, marked.
Gametes : *Short & Angora, normal & albino, grey & black, self & Dutch.*

No. 11. ♀ (1 × 2) : Short, normal, grey, self.
Gametes : *Short & Angora, normal & albino, grey & black, self.*

No. 12. ♂ (1 × 2) : Short, normal, grey, self.
Gametes : *Short & Angora, normal & albino, grey & black, self.*

No. 14. ♂ (5 × 2) : Short, albino, white.
Gametes : *Short & Angora, albino, black, self.*

No. 15. ♀ (8 × 2) : Angora, albino, white.
Gametes : *Angora, albino, grey & black, self & Dutch.*

No. 16. ♀ (7 × 2) : Angora, albino, white.
Gametes : *Angora, albino, grey & black, self & Dutch.*

No. 17. ♀ (7 × 2) : Short, normal, grey, self.
Gametes : *Short & Angora, normal & albino, grey & black, self.*

No 18. ♀ (7 × 2) : Short, normal, grey, self.
Gametes : *Short & Angora, normal & albino, grey & black, self.*

No. **19.** ♀ (5 × 2) : Short, normal, black, self.
GAMETES : *Short & Angora, normal & albino, black, self.*

No. **20.** ♀ (5 × 2) : Angora, normal, black, marked.
GAMETES : *Angora, normal & albino, black, self.*

No. **21.** ♀ (5 × 2) : Short, normal, black, marked.
GAMETES : *Short & Angora, normal & albino, black, self.*

No. **22.** ♀ (1 × 4) : Short, normal, grey, self.
GAMETES : *Short, normal, grey, self.*

No. **23.** ♀ (3 × 2) : Angora, albino, white.
GAMETES : *Angora, albino, grey & black, self & Dutch.*

No. **24.** ♂ (3 × 2) : Angora, albino, white.
GAMETES : *Angora, albino, black, self & Dutch.*

No. **25.** ♂ (1 × 4) : Short, normal, grey, self.
GAMETES : *Short, normal, grey, self.*

No. **26.** ♂ (11 × 12) : Angora, normal, grey, self.
GAMETES : *Angora, normal & albino, grey & black, self.*

No. **27.** ♂ (9 × 10) : Short, normal, grey, marked.
GAMETES : *Short & Angora, normal & albino, grey & black, self & Dutch.*

No. **28.** ♂ (9 × 10) : Short, normal, black, marked.
GAMETES : *Short & Angora, normal, black, self & Dutch.*

No. **29.** ♀ (9 × 10) : Short, normal, grey, marked.
GAMETES : *Short & Angora, normal & albino, grey & black, self & Dutch.*

No. **30.** ♀ (11 × 12) : Short, normal, grey, self.
GAMETES : *Short, normal, grey & black, self.*

No. **31.** ♀ (11 × 12) : Short, normal, grey, self.
GAMETES : *Short & Angora, normal & albino, grey & black, self.*

No. **32.** ♀ (11 × 12) : Short, normal, grey, self.
GAMETES : *Short, normal, grey & black, self.*

No. **33.** ♀ (11 × 12) : Angora, normal, black, self.
GAMETES : *Angora, normal & albino, black, self.*

No. **34.** ♀ (11 × 12) : Short, albino, white.
GAMETES : *Short, albino, grey & black, self.*

No. **35.** ♀ (9 × 10) : Short, normal, grey, self.
GAMETES : *Short & Angora, normal, grey & black, self.*

No. **36.** ♀ (9 × 10) : Short, normal, grey, self.
GAMETES : *Short, normal & albino, grey, self.*

No. **37.** ♂ (7 × 10) : Angora, normal, grey, Dutch.
GAMETES : *Angora, normal & albino, grey, Dutch.*

No. **38.** ♂ (7 × 10) : Short, albino, white.
GAMETES : *Short, albino, grey & black, self.*

No. **39.** ♀ (7 × 10) : Short, albino, white.
GAMETES : *Short & Angora, grey & black, self.*

No. **41.** ♂ (3 × 10) : Angora, normal, black, Dutch.
GAMETES : *Angora, normal & albino, black, Dutch.*

No. **42.** ♀ (8 × 2) : Angora, normal, grey, self.
GAMETES : *Angora, normal & albino, grey & black, self.*

No. **43.** ♀ (1 × 12) : Short, normal, grey, self.
GAMETES : *Short, normal, grey, self.*

No. **44.** ♀ (1 × 12) : Short, normal, grey, self.
GAMETES : *Short & Angora, normal, grey & black, self.*

No. **45.** ♀ (5 × 2) : Short, albino, white.
GAMETES : *Short & Angora, albino, black, self.*

No. **50.** ♀ (Pure Angora) : Angora, albino, white.
GAMETES : *Angora, albino, grey & black, self.*

No. **53.** ♀ (7 × 10) : Angora, normal, grey, Dutch.
GAMETES : *Angora, normal & albino, grey, Dutch.*

No. **54.** (9 × 10) : Angora, normal, black, Dutch.
GAMETES : *Angora, normal & albino, black, Dutch.*

CONCLUSIONS.

A study of the somatic characters and gametic factors of the above individuals brings out the important fact that certain individuals, identical in appearance and with precisely the same ancestry, differ, in a regular and permanent manner, in their breeding potentialities (*e. g.* Nos. 35 & 36).

In such cases it is evident that neither the outward appearance of the individual nor a knowledge of its ancestry is a safe guide to its breeding potentialities (it is only in the case of recessive characters, of any ancestry, that the soma is a true guide), while, on the other hand, as the above experiments show, a knowledge of its gametic constitution and of the various dominances provides a sure guide.

Once the gametic formula of each individual has been determined by Mendelian analysis, the future results of any matings can be foreseen with accuracy, whereas a knowledge simply of the somatic characters of an individual and its ancestors is altogether unavailing.

The true measure of heredity therefore is neither the somatic character of the individual nor of its ancestors, but its gametic constitution, and, in our present state of knowledge, this can only be determined by experimental breeding on Mendelian lines.

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Postscript.

The Mendelian Principles of Heredity.

The classical experiments with Peas completed by Mendel in 1865 led him to the following conceptions of heredity *.

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* For English translation of Mendel's papers and further details see Bateson's 'Mendel's Principles of Heredity' (Cambridge University Press, 1902).

A plant is composed of unit characters which are represented in the germ-cells, or gametes, by independent factors.

Pure breeding involves the union of *like* factors: (A × A = A A).

Cross breeding involves the union of *unlike* (but corresponding) factors: (A × B = A B).

Pure races give off gametes carrying the one factor concerned: (A A gives off A_s simply).

Hybrid races give off two kinds of gametes, on the average in equal numbers, each carrying one of the factors concerned in the cross. *No gamete carries both* (A B gives off A_s and B_s in equal numbers, and no gamete carries A and B).

This is known as gametic segregation.

From this it follows that the offspring of the self-fertilized hybrids A B are of three kinds:—25 per cent. A A, 50 p. c. A B, and 25 p. c. B B.

The A A_s and B B_s, being gametically pure, breed true notwithstanding their A B origin.

This is known as gametic purity.

The A B_s, being hybrids, breed as such, gametic segregation again taking place.

When more than one pair of unit characters are concerned in the cross, the average result can be calculated on the above basis by the simple calculus of chance.

In his experiments Mendel encountered the phenomenon of dominance, *i. e.* when certain pairs of unit characters were crossed, one of the pair was always dominant over the other, which Mendel termed recessive: A × B = A (B).

This dominance of A over B in the soma caused the offspring of the self-fertilized hybrids to appear as 3 A : 1 B. Analysis in the following generation, however, demonstrated their gametic formula to be 1 A A : 2 A B : 1 B B, in accordance with the Mendelian principles.

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